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Total number of authors:  
11

Published in:  
Journal of Plankton Research

Link to article, DOI:  
[10.1093/plankt/fby007](https://doi.org/10.1093/plankt/fby007)

Publication date:  
2018

Document Version  
Peer reviewed version

[Link back to DTU Orbit](#)

### Citation (APA):

Cornwell, L. E., Findlay, H. S., Fileman, E. S., Smyth, T. J., Hirst, A. G., Bruun, J. T., McEvoy, A. J., Widdicombe, C. E., Castellani, C., Lewis, C., & Atkinson, A. (2018). Seasonality of *Oithona similis* and *Calanus helgolandicus* reproduction and abundance: contrasting responses to environmental variation at a shelf site. *Journal of Plankton Research*, 40(3), 295-310. <https://doi.org/10.1093/plankt/fby007>

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**Seasonality of *Oithona similis* and *Calanus helgolandicus* reproduction and abundance: contrasting responses to environmental variation at a shelf site**

Cornwell, L. E.<sup>1</sup>

Findlay, H. S.<sup>1</sup>

Fileman, E. S.<sup>1</sup>

Smyth, T. J.<sup>1</sup>

Hirst, A. G.<sup>3,4</sup>

Bruun, J. T.<sup>5,6</sup>

McEvoy, A. J.<sup>1</sup>

Widdicombe, C. E.<sup>1</sup>

Castellani, C.<sup>1</sup>

Lewis, C.<sup>2</sup>

Atkinson, A.<sup>1,\*</sup>

<sup>1</sup>Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth, PL1 3DH, UK

<sup>2</sup>College of Life and Environmental Sciences, University of Exeter, Hatherly Laboratories, Prince of Wales Road, Exeter, EX4 4PS, UK

<sup>3</sup> School of Environmental Sciences, University of Liverpool, Liverpool, L69 3GP, UK

<sup>4</sup> Centre for Ocean Life, National Institute for Aquatic Resources, Technical University of Denmark, Kavalergarden 6, Charlottenlund 2920, Denmark

<sup>5</sup> Sweet Briar, Totnes, TQ9 5LH, UK

<sup>6</sup> Formerly at Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth, PL1 3DH, UK

\*Corresponding author: Angus Atkinson, Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth, PL1 3DH, UK. Email: [aat@pml.ac.uk](mailto:aat@pml.ac.uk)

26   **Abstract**

27   The pelagic copepods *Oithona similis* and *Calanus helgolandicus* have overlapping geographic  
28   ranges, yet contrast in feeding mode, reproductive strategy, and body size. We investigate how  
29   these contrasting traits influence the seasonality of copepod abundance and reproductive output  
30   under environmental variation, using time series data collected over 25 years at the Western  
31   Channel Observatory station L4. The proportional change in Egg Production Rate (EPR, eggs  
32   female<sup>-1</sup> d<sup>-1</sup>) over the annual cycle was ~10-fold and similar for both species, although EPR of *O.*  
33   *similis* was only ~ 11% that of *C. helgolandicus*. The timing of EPR maxima for *O. similis*  
34   coincided with increased Sea Surface Temperature (SST) in summer, likely due to a temperature-  
35   dependent brooding period. Conversely, EPR of broadcast spawning *C. helgolandicus* was more  
36   strongly related to Net Heat Flux (NHF) and diatom biomass, both parameters associated with the  
37   spring phytoplankton bloom. In both species, female body mass negatively correlated with SST,  
38   with a 7.5% reduction in body mass per °C in *C. helgolandicus* compared to just 2.3% in *O. similis*.  
39   Finally, seasonality of EPR and adult and copepodite abundance was strongly decoupled in both  
40   species, suggesting that optimum conditions for reproduction and abundance occur at different  
41   times of the year.

42   **Keywords:** functional trait, egg production rate, *Oithona similis*, *Calanus helgolandicus*, Western  
43   Channel Observatory.

## 44    **Introduction**

45            Functional traits are characteristic features of an organism that impact fitness by mediating  
46    growth, reproduction, and survival (Litchman *et al.*, 2013). Such traits can be used to identify links  
47    between population responses and the processes that drive them (McGill *et al.*, 2006). For major  
48    copepod species, much of our biological knowledge on their dynamics has been based on single  
49    species studies. Examples of such studies for the cyclopoid *Oithona similis* include Sabatini and  
50    Kiørboe (1994); Fransz and Gonzalez (1995); Castellani *et al* (2005a); Dvoretsky and Dvoretsky  
51    (2009a,b). The calanoid *Calanus helgolandicus* overlaps in range with *O. similis* but contrasts in  
52    several key traits. However, knowledge of these traits is again based heavily on autecological  
53    studies (e.g. Pond *et al.*, 1996; Irigoien *et al.*, 2000a,b; Irigoien and Harris, 2003; Rey-Rassat *et al.*,  
54    2004; Maud *et al.*, 2015). Despite recent establishment of copepod trait databases (Benedetti *et al.*,  
55    2015; Brun *et al.*, 2017) and meta-analyses (Horne *et al.*, 2016), it remains difficult to identify the  
56    degree to which contrasts in feeding and egg production rates (Benedetti *et al.*, 2015; Brun *et al.*,  
57    2016; 2017), or temperature-body size response (Horne *et al.*, 2016), represent genuine contrasts in  
58    functional traits, or simply differences in environmental conditions between the respective studies.

59            To address this issue, we make a direct comparison of two dominant, co-existing species,  
60    *Oithona similis* and *Calanus helgolandicus*. Our study is based on the L4 time series site, a shallow,  
61    stratifying shelf site in the Western English Channel (Harris, 2010). *O. similis* is thought to exert  
62    minimal energy waiting for motile prey, such as ciliates and dinoflagellates, to enter detection range  
63    (Kiørboe, 2011). Conversely, *C. helgolandicus* is an active feeder, generating feeding currents  
64    suited to catching non-motile, diatom prey (Kiørboe, 2011). Egg Production Rate (EPR, eggs  
65    female<sup>-1</sup> d<sup>-1</sup>) in brooding species such as *O. similis*, may become limited by the fact that a new  
66    clutch cannot be laid until the previous eggs hatch (Ward and Hirst, 2007). Increased temperature  
67    increases embryonic development rate, thus potentially decreasing the time from the production of  
68    one clutch to the next (Nielsen *et al.*, 2002), and facilitating greater egg production rates in warmer

69 temperatures. In contrast, EPR in *C. helgolandicus*, a broadcast spawning species, is not restricted  
70 in the same way by the time interval between clutches, and therefore its fecundity may be less  
71 temperature dependent.

72 Temperature may also have a series of other direct and indirect effects on copepod  
73 population dynamics. One reason for this is that temperature impacts metabolism through its effects  
74 on rates of biochemical reactions (Gillooly *et al.*, 2001). For example, increased respiration rate  
75 with temperature has been observed in *Oithona similis* (Castellani *et al.*, 2005b) and *Calanus*  
76 *helgolandicus* (Hirche, 1983). Furthermore, ectothermic organisms generally mature to a smaller  
77 body size under increased temperature conditions (Atkinson, 1994; Forster *et al.*, 2012), as has been  
78 observed for female *O. similis* (Castellani *et al.*, 2007), and *C. helgolandicus* (Bonnet *et al.*, 2009).  
79 The temperature range over which such effects occur, as well as the thermal optima for  
80 reproduction and development, vary between copepod species and geographic populations  
81 (Halsband-Lenk *et al.*, 2002). The effects of temperature on copepod populations will indirectly  
82 effect their prey, by altering feeding rate (Dam and Peterson, 1988), and inducing phenological  
83 shifts in copepod populations (Atkinson *et al.*, 2015). Overall, temperature is thus an important  
84 parameter to consider when investigating ecosystem dynamics.

85 Another physical variable connected both to temperature and plankton seasonality, is the  
86 Net Heat Flux (NHF) between the atmosphere and the ocean (Smyth *et al.*, 2014). NHF  
87 incorporates air-sea temperature difference, alongside irradiance, wind speed, and water column  
88 stratification, all of which are major factors that can affect plankton community at the Western  
89 Channel Observatory (WCO) coastal station L4 (Smyth *et al.*, 2014). Water column stratification in  
90 spring increases the residence time of phytoplankton in the euphotic layer (Taylor and Ferrari,  
91 2011; Smyth *et al.*, 2014), facilitating the spring phytoplankton bloom. The autumn transition to  
92 negative NHF is associated with the restriction in phytoplankton growth due to shortened day-  
93 length, lower irradiance, and turbulent mixing limiting residence times in the euphotic layer.

94           In measuring the response of copepods to this seasonality, Egg Production Rate (EPR)  
95   provides an index of female copepod performance, as it integrates energy uptake and assimilation.  
96   Meanwhile, changes in population abundance over time are driven by changes in both recruitment  
97   and mortality rates (Hirst and Kiørboe, 2002). *Calanus helgolandicus* EPR at station L4 has been  
98   monitored on a weekly basis since 1992, an extensive dataset to which our study contributes new  
99   data on the contrasting species *Oithona similis*. The strong seasonality at L4 makes it an ideal site  
100   for studying the impact of environmental variation on copepod population dynamics.

101           Our study tests two hypotheses: 1) EPR in *Oithona similis* has a stronger relationship with  
102   Sea Surface Temperature (SST), compared to *Calanus helgolandicus*, due to its temperature-  
103   dependent brooding period; and 2) *O. similis* EPR has a stronger relationship with the biomass of  
104   motile prey, while *C. helgolandicus* EPR has a stronger relationship with the biomass of non-motile  
105   prey. To test these hypotheses we used Generalised Additive Mixed Models (GAMMs) to examine  
106   and identify the non-linear relationships between the environment and EPR for *O. similis* and *C.*  
107   *helgolandicus*. This is an accurate identification approach that accounts for noise autocorrelation  
108   (Hastie and Tibshirani, 1990; Young *et al.*, 2001; Bruun *et al.*, 2017). We used these models to  
109   detect the threshold value of the independent variables (SST, NHF, and prey biomass), where it  
110   starts to show a significant effect on EPR. Further, we examined the seasonality of adult female and  
111   copepodite abundance, and female and egg carbon mass.

## 112    **Methods**

113    The Western Channel Observatory (WCO) station L4 is 13 km SSW of Plymouth, and has been  
114    sampled by Plymouth Marine Laboratory (PML) on a weekly basis since 1988 (Harris, 2010). There  
115    is a large amount of knowledge on the conditions at L4, with numerous publications in the literature  
116    on the L4 plankton community (e.g. Eloire *et al.*, 2010; Highfield *et al.*, 2010; Widdicombe *et al.*,  
117    2010; Atkinson *et al.*, 2015; White *et al.*, 2015, and references therein). The variables explored in  
118    this study, and the time period over which they have been measured, are summarised in **Table I**.  
119    Access to the most updated versions of the WCO time series data is available from Plymouth  
120    Marine Laboratory upon request (<http://www.westernchannelobservatory.org.uk/>). Original data for  
121    *Oithona similis* are provided in the Supplementary Material.

## 122    **Physical parameters**

123            Sea Surface Temperature (SST) and surface Chlorophyll *a* concentration [Chl *a*] were  
124    measured as part of the ongoing WCO time series. SST was measured with a mercury in glass  
125    thermometer until 1993. Between 1993 and 2002, SST was recorded electronically using CTD  
126    sensors. Since 2002, SST has been determined using a SeaBird SBE 19+ CTD, attached to a vertical  
127    profiler. [Chl *a*] was obtained by filtering 100 mL of surface seawater through 25 mm GF/F filters  
128    in triplicate, extracting in 90% acetone at 4°C, then analysing by Turner fluorometry, following  
129    Welschmeyer (1994). Datasets for water column temperature and surface [Chl *a*] at L4 are publicly  
130    available at the above mentioned WCO website.

131            Net Heat Flux (NHF) was determined between 1992 and 2016 using the methodology of  
132    Smyth *et al* (2014), as follows. Four processes control air-sea heat flux: shortwave radiation from  
133    the sun ( $Q_{SW}$ ), outgoing longwave radiation from the sea surface ( $Q_{LW}$ ), sensible heat transfer  
134    resulting from air-sea temperature differences ( $Q_{SH}$ ), and latent heat transfer via evaporation of sea  
135    water ( $Q_{LH}$ ). The Woods Hole Oceanographic Institution air-sea exchange Matlab tools (Fairall *et*  
136    *al.*, 2003) were used to determine  $Q_{SW}$ ,  $Q_{LW}$ ,  $Q_{SH}$  and  $Q_{LH}$  (Pawlowicz *et al.*, 2001), in units of W

137  $\text{m}^{-2}$ . Meteorological parameters were obtained from the European Centre for Medium Range  
138 Weather Forecasting (ECMWF) ERA-40 and Operational analyses, extracted for the grid point 50  
139  $^{\circ}\text{N}$ , 4  $^{\circ}\text{W}$ . These parameters were: air temperature ( $T_a$ ,  $^{\circ}\text{C}$ ), dew point ( $T_d$ ,  $^{\circ}\text{C}$ ), wind-speed at 10 m  
140 ( $U_{10}$ ,  $\text{ms}^{-1}$ ), cloud fraction (CF, 0: clear; 1: overcast) and atmospheric pressure (P, mb). SST ( $T_s$ ,  
141  $^{\circ}\text{C}$ ), combined with the ECMWF data, was used to run the heat flux model for the period 1992 –  
142 2016.  $Q_{\text{SW}}$  was calculated as a function of date and position with correction for CF (Reed, 1977);  
143  $Q_{\text{LW}}$  as a function of  $T_a$ ,  $T_s$ ,  $T_d$ , CF using the Berliand bulk formula (Fung *et al.*, 1984).  $Q_{\text{SH}}$  and  
144  $Q_{\text{LH}}$  were calculated as a function of  $T_a$ ,  $T_s$ ,  $T_d$ , CF, P,  $U_{10}$ . The sum of all four components results  
145 in NHF, with the sign convention of positive NHF being heat flux into the water column.

#### 146 **Plankton sampling**

147 Plankton samples were collected using vertical net hauls from 50 m (sea floor depth ~ 54 m) to the  
148 surface. *Oithona similis* data were from samples collected in 2003, and from November 2011 to  
149 December 2016. Samples from 2003 were collected using a 50  $\mu\text{m}$  mesh, 50 cm diameter ring net,  
150 from which samples were fixed in 4% buffered formalin. Samples from 2011 - 2014 were collected  
151 using a 63  $\mu\text{m}$  mesh, 57 cm diameter ring net, and the plankton fixed as described above. Samples  
152 from 2015 - 2016 were collected using the 63  $\mu\text{m}$  mesh ring net, and 250 mL sub-samples were  
153 fixed in 2% acid Lugol's solution. Samples for *Calanus helgolandicus* abundance were collected  
154 using a 200  $\mu\text{m}$  mesh, 57 cm diameter, WP2 net (UNESCO, 1968). Live, non-quantitative net hauls  
155 for *C. helgolandicus*, for Egg Production Rate (EPR) incubations throughout the period 1992 –  
156 2016, were collected with a 710  $\mu\text{m}$  mesh ring net of 45 cm diameter, towed obliquely throughout  
157 the top 10 m layer at 1 - 2 knots.

158 Weekly sampling for phytoplankton and protozooplankton has also been undertaken at L4  
159 since 1992. Samples were collected from 10 m with a 10 L Niskin bottle. For each sampling event,  
160 a 200 mL sub-sample was fixed with 2% acid Lugol's solution, and another 200 mL sub-sample was



161 fixed in 4% neutral formaldehyde for enumerating coccolithophores. Further detail on the methods  
162 can be found in Widdicombe *et al* (2010).

### 163 **Plankton analysis**

164 All data on *Oithona similis* were derived separately from the WCO core time series datasets, as  
165 detailed information on this species had not been previously recorded at L4. The 63 µm net samples  
166 fixed in 4% buffered formalin were screened through a 50 µm mesh, and the retained organisms re-  
167 suspended in tap water, made up to a known volume. The re-suspended sample was then pipetted  
168 into a 3 mL Hydrobios<sup>®</sup> counting chamber. The 63 µm net samples fixed in 2% acid Lugol's  
169 solution were settled, and the top 200 mL removed via a syringe. The remaining 50 mL sample was  
170 left to settle for 3 hours in the counting chamber. Highly concentrated Lugol's samples were  
171 thoroughly mixed, before a 25 mL sub-sample was removed and settled for 1 hour. Prepared  
172 samples were then analysed under an Olympus IMT-2 inverted microscope at 40 x magnification,  
173 and the number of adult males and females, juvenile copepodites, and egg sacs, were enumerated.  
174 As most egg sacs were detached from the females in all samples, both detached and attached egg  
175 sacs were enumerated. Copepodite abundance may be slightly overestimated due to the presence of  
176 the congener *O. nana*, the copepodites of which are difficult to distinguish from *O. similis*.  
177 However, *O. nana* abundance made up only ~ 7% of total *Oithona* abundance. *O. similis* females  
178 typically carry two egg sacs, thus ovigerous female abundance was determined by halving egg sac  
179 abundance (Uye and Sano, 1995). The number of eggs per sac was recorded from a randomly  
180 selected subset of 10 egg sacs in each sample. Egg sacs were transparent, thus not requiring  
181 dissection (Drif *et al.*, 2010). Regrettably, naupliar abundance could not be quantitatively  
182 determined from the net samples, thus our data do not include this component of the total *O. similis*  
183 population.

184 Female prosome length and egg diameter of *Oithona similis* were measured under an  
185 Olympus IMT-2 inverted microscope at 100 x magnification using an eye-piece graticule. Prosome

length was taken from the anterior margin of the prosome to the posterior of the 4<sup>th</sup> thorax segment, where the articulation exists, following Uye (1982). Prosome length was measured for 10 females per sample, or for all females when less than 10 were present, and converted into female carbon mass (Cf,  $\mu\text{g C female}^{-1}$ ) using length-mass relationships in Uye (1982). Egg diameter was measured from 2 - 3 eggs per sac, and converted to egg carbon mass (Ce,  $\mu\text{g C egg}^{-1}$ ) (Uye and Sano, 1995). To calculate the percent change in Cf per °C, the slope of the linear regression plot of the natural Log (ln) Cf against SST was transformed using the equation of Forster *et al* (2012). All equations for *O. similis* carbon mass calculations are provided in **Table II**.

Female and copepodite abundance data for *Calanus helgolandicus* were obtained from the WCO time series from 1992 – 2016. *C. helgolandicus* is the dominant *Calanus* species at L4. *Calanus* copepodite abundance data may include *C. finmarchicus*, although considering *C. finmarchicus* comprises a median of just 4% of *C. helgolandicus* abundance throughout the water column at L4 (Maud *et al.*, 2015), we therefore made the simplifying assumption that all counted individuals were *C. helgolandicus*. For the purpose of comparison, we used carbon mass data of Pond *et al* (1996) for *C. helgolandicus* females and eggs, at L4 as measured over the period March - September 1994. To calculate the percent change in female carbon mass per °C, we used the same equation as for *O. similis* (following Forster *et al.*, 2012) (**Table II**). Once again, naupliar abundance could not be quantitatively measured from the 200  $\mu\text{m}$  net samples, and so once again our data do not include these in our total *C. helgolandicus* population abundances.

Phytoplankton and protozooplankton time series data were available from 1992 – 2014, from which we derived biomass data for the following functional groups; diatoms, phyto- and zooflagellates, auto- and heterotrophic dinoflagellates, ciliates, and coccolithophores. All cells > 2  $\mu\text{m}$  were identified, to species level where possible, and enumerated at either 200 or 400 x magnification using an inverted microscope. Phyto- and zooflagellates are typically 2 - 10  $\mu\text{m}$ , and were separated based on the presence or absence of chloroplasts. Cell measurements were used to

211 calculate taxa-specific mean cell biovolume according to appropriate geometric shapes (Kovala and  
212 Larrance, 1966) and converted to biomass using the equations of Menden-Deuer and Lessard  
213 (2000). For further detail we refer the reader to Widdicombe *et al* (2010).

#### 214 **Egg Production Rate (EPR)**

215 *In situ* EPR (eggs female<sup>-1</sup> d<sup>-1</sup>) of *Oithona similis* was calculated from female and egg sac  
216 abundance, and the number of eggs per sac, using the egg ratio method (Edmondson *et al.*, 1962;  
217 Checkley, 1980). To account for the effect of female body size, mass-specific EPR (SEPR, egg-C  
218 female-C<sup>-1</sup> d<sup>-1</sup>) was calculated utilising our measures of prosome length together with prosome  
219 length-mass equations (Uye, 1982) and egg diameter (Uye and Sano, 1995). All equations for *O.*  
220 *similis* EPR and SEPR are provided in (**Table II**).

221 *Calanus helgolandicus* EPR has been determined since 1992 using the following protocol.  
222 After each sampling event, live samples were transported to the laboratory in a cool box within 2 –  
223 3 h of collection, and 25 mature females were picked from the sample and five replicates of five  
224 females were incubated. To prevent cannibalism of the eggs, females for each replicate were placed  
225 in a 500 µm mesh-bottom Plexiglas chamber inside a 2 L plastic beaker filled with 1.5 L of 0.2 µm  
226 filtered seawater, at ambient SST and constant darkness for 24 h. Eggs from each replicate were  
227 counted and EPR calculated (Maud *et al.*, 2015). *C. helgolandicus* SEPR was calculated using the  
228 carbon mass data of Pond *et al* (1996) for *C. helgolandicus* at L4 during March - September 1994,  
229 by multiplying EPR by egg carbon content (µg C egg<sup>-1</sup>), then dividing the product by female carbon  
230 mass (µg C female<sup>-1</sup>), for all corresponding dates.

#### 231 **Statistics**

232 Statistical analysis was performed in R (version 3.02.1, R Development Core Team, 2016). A *t* -  
233 test was run to test the difference between the full *Calanus helgolandicus* EPR dataset, and a dataset  
234 comprising just the dates compatible with the *Oithona similis* dataset. The strength of the

relationship between EPR and SEPR in both species was assessed using the Pearson's correlation coefficient. Generalised Additive Mixed Models (GAMMs) were run using the function 'gamm' from the R package 'mgcv' (Wood, 2006), to determine the relationships between EPR and the physical environment and trophic interaction terms. GAMMs were chosen for their greater capacity to identify non-linear relationships compared to Generalised Linear Models (GLMs). The GAMM also accommodates Auto Regressive (AR) and Moving Average (MA) noise, and so together this approach provided an unbiased fit for our data. The models were selected based on Akaike Information Criterion (AIC), choosing the model with the lowest AIC value while maintaining a complete physical environment and trophic interaction model structure. Autocorrelation function (ACF) and partial autocorrelation function (PACF) plots of the raw and standardised residuals indicated that an AR of order 3 was required for the *C. helgolandicus* time series to account for temporal autocorrelation. The GAMM was used to analyse the *O. similis* dataset for the contiguous years of 2011 to 2016. The year 2003 was excluded to remove the gap in the time series. An autoregressive model was not selected for the *O. similis* dataset as the ACF evidence was less certain: the relatively short duration record means the selection of ARMA noise terms would be less accurate. A white noise model was selected in this case. For further detail on this type of non-linear process identification and statistical analysis approaches, see Bruun *et al* (2017), Tarran and Bruun (2015), and Young *et al* (2001). Non-significant relationships between EPR and the environmental parameters analysed in this study are not presented.

## 254    **Results**

### 255    **L4 dynamics**

256    The environmental conditions at L4 varied inter-annually, but maintained general seasonal trends.  
257    Sea Surface Temperature (SST) increased from  $\sim 9^{\circ}\text{C}$  in March to  $\sim 16^{\circ}\text{C}$  in August (**Fig. 1**). From  
258    March – September there was a positive Net Heat Flux (NHF) into the water column, peaking in  
259    June at  $\sim 180 \text{ W m}^{-2}$ , followed by a transition to negative NHF, becoming most negative in  
260    December at  $\sim -115 \text{ W m}^{-2}$  (**Fig. 1**). Pre-spring bloom total Chlorophyll *a* concentration [Chl *a*] was  
261     $\sim 0.6 \mu\text{g L}^{-1}$ , and increased during the spring bloom to  $\sim 2 \mu\text{g L}^{-1}$  (**Fig. 2**). Diatom blooms occurred  
262    predominantly in spring, sometimes continuing into autumn. Ciliate and phytoflagellate biomass  
263    was generally highest in late spring, followed by biomass peaks for heterotrophic dinoflagellates  
264    and zooflagellates in the summer, and autotrophic dinoflagellates and coccolithophores in autumn  
265    (**Fig. 2**).

### 266    **Physical and trophic effects on *Oithona similis* egg production**

267    Egg Production Rate (EPR) and mass-specific EPR (SEPR) of *Oithona similis* were strongly  
268    correlated (Pearson's correlation coefficient,  $\rho = 0.98$ ). Maximum mean ( $\pm$  SE) EPR occurred in  
269    August ( $3.29 \pm 0.95 \text{ eggs female}^{-1} \text{ d}^{-1}$ ), and was lowest in December ( $0.35 \pm 0.09 \text{ eggs female}^{-1} \text{ d}^{-1}$ )  
270    (**Fig. 1**). Thus, the proportional change of EPR over an annual cycle had an almost 10-fold range,  
271    and a coefficient of variation of 89.7%. EPR increased with SST, with this relationship becoming  
272    significant at  $\sim 15^{\circ}\text{C}$  (**Fig. 3, Table III**), indicating rapid increase in EPR above this threshold  
273    temperature. The only other variable to show a clear significant relationship with *O. similis* EPR  
274    was NHF (**Table III**), with the positive relationship between EPR and NHF becoming significant  
275    above  $\sim 200 \text{ W m}^{-2}$  (**Fig. 3**), at the point of maximum positive NHF into the water column (**Fig. 1**).

276            No significant relationship occurred between *Oithona similis* EPR and the biomass of any  
277    phyto- protozooplankton taxa that we considered. Therefore, in order to provide a trophic

278 interaction term, [Chl *a*] was included in the GAMM, although this term did not have an overall  
279 significant relationship with EPR (**Table III**). The GAMM plot shows [Chl *a*] had a large  
280 uncertainty interval, although it may have a marginally significant relationship with EPR at [Chl *a*]  
281 below  $\sim 0.9 \mu\text{g L}^{-1}$  (**Fig. 3**).

#### 282 ***Oithona similis* abundance**

283 Mean ( $\pm$  SE) female abundance was highest in March ( $286 \pm 111 \text{ ind m}^{-3}$ ), and lowest in December  
284 ( $49 \pm 15 \text{ ind m}^{-3}$ ) (**Fig. 4**). Similarly, mean egg sac abundance was highest in April ( $172 \pm 28 \text{ ind m}^{-3}$ )  
285 and lowest in December ( $9 \pm 3 \text{ ind m}^{-3}$ ) (**Fig. 4**). Mean copepodite abundance had two peaks, the  
286 largest in March ( $737 \pm 198 \text{ ind m}^{-3}$ ) followed by a smaller peak in August, and abundance was  
287 again lowest in December ( $152 \pm 32 \text{ ind m}^{-3}$ ) (**Fig. 4**). The proportion of ovigerous females in the  
288 total female population ranged from  $\sim 9\%$  in December to  $\sim 30\%$  throughout February - September.  
289 Mean male abundance also peaked in March ( $42 \pm 22 \text{ ind m}^{-3}$ ), but was lowest in October ( $4 \pm 2 \text{ ind}$   
290  $\text{m}^{-3}$ ). There was a strong female-biased sex ratio, with a mean female: male abundance ratio of 10,  
291 although this varied considerably over time.

#### 292 ***Oithona similis* body size variation**

293 Females were observed to have largest body sizes in May ( $0.41 \pm 0.01 \mu\text{g C female}^{-1}$ ), and were  
294 smallest in November ( $0.33 \pm 0.004 \mu\text{g C female}^{-1}$ ) (**Fig. 5**). Female carbon mass (Cf) negatively  
295 correlated with SST (**Fig. 6**), exhibiting a mean ( $\pm 95\%$  CI) percent change of  $-2.33 \pm 0.5\%$  in Cf  
296 per  $^{\circ}\text{C}$  increase in SST. Egg carbon mass (Ce) showed no clear seasonality, with a mean ( $\pm$  SE) of  
297  $0.014 \pm 0.001 \mu\text{g C egg}^{-1}$  throughout the year (**Fig. 5**), and was not significantly correlated with Cf,  
298 or the number of eggs per sac. The mean ( $\pm$  SE) values of these parameters are provided in **Table**  
299 **IV**.

#### 300 **Physical and trophic effects on *Calanus helgolandicus* egg production**

301 The seasonality of EPR and SEPR were very similar (Pearson's correlation coefficient,  $\rho = 0.88$ )  
 302 (**Fig. 1**), at least during 1994, the year for which carbon data were available (Pond *et al.*, 1996).  
 303 There was no significant difference in EPR seasonality between the full *Calanus helgolandicus*  
 304 dataset and the one comprising just the dates compatible in time with the values for *Oithona similis*,  
 305 thus we use the full dataset in our comparisons. Mean ( $\pm$  SE) EPR was highest throughout April –  
 306 June ( $24.8 \pm 1.1$  eggs female<sup>-1</sup> d<sup>-1</sup>), and lowest in December ( $3.14 \pm 0.52$  eggs female<sup>-1</sup> d<sup>-1</sup>) (**Fig. 1**).  
 307 The proportional change of EPR over the year therefore showed an approximate 8-fold range, and a  
 308 coefficient of variation of 73.6%. There was a strong relationship between EPR and NHF (**Table**  
 309 **V**), with a significant positive effect occurring for NHF above  $\sim 50 \text{ W m}^{-2}$  (**Fig. 7**). No significant  
 310 relationship was found between *C. helgolandicus* EPR and SST. The *C. helgolandicus* EPR and  
 311 diatom biomass analysis indicated a logarithmic relationship, which was significant at diatom  
 312 biomass between 20 - 60 mg C m<sup>-3</sup> (**Fig. 7, Table V**). Once diatom biomass exceeded  $\sim 60 \text{ mg C m}^{-3}$ ,  
 313 the relationship became non-significant. Analysis also showed a marginally significant  
 314 relationship between EPR and heterotrophic dinoflagellates, which appeared to take a logarithmic  
 315 form, with the relationship becoming positive after heterotrophic dinoflagellate biomass reached  $\sim 5$   
 316 mg C m<sup>-3</sup> (**Fig. 7, Table V**). We note that the relationship between EPR and heterotrophic  
 317 dinoflagellate biomass shows a significant non-linear effect with a wide uncertainty interval (**Fig.**  
 318 **7**). No significant relationship was found between *C. helgolandicus* EPR and [Chl *a*].

#### 319 *Calanus helgolandicus* abundance

320 Mean ( $\pm$  SE) female abundance was highest in June ( $20 \pm 3$  ind m<sup>-3</sup>) and lowest in November ( $2 \pm$   
 321  $0.2$  ind m<sup>-3</sup>) (**Fig. 4**). Mean copepodite abundance was considerably higher, peaking in August ( $176$   
 322  $\pm 37$  ind m<sup>-3</sup>), with minimum values in December ( $13 \pm 3$  ind m<sup>-3</sup>) (**Fig. 4**). Mean male abundance  
 323 was also highest in June ( $6 \pm 3$  ind m<sup>-3</sup>) and lowest in December ( $0.3 \pm 0.07$  ind m<sup>-3</sup>).

#### 324 *Calanus helgolandicus* body size variation

325 Based on published carbon mass data at L4 extracted from Pond *et al* (1996) and measured between  
326 March and September in 1994, mean ( $\pm$  SE) female carbon mass (Cf) was highest in April ( $64 \pm 2$   
327  $\mu\text{g C female}^{-1}$ ), and lowest in August ( $33 \pm 1 \mu\text{g C female}^{-1}$ ) (**Fig. 5**), and thus negatively correlated  
328 with SST (**Fig. 6**), with a mean ( $\pm$  95% CI) percent change of  $-7.46 \pm 1.6\%$  in Cf per  $^{\circ}\text{C}$  increase in  
329 SST. Egg carbon mass (Ce) peaked in April ( $0.64 \pm 0.04 \mu\text{g C egg}^{-1}$ ), with minimum values in  
330 September ( $0.23 \pm 0.01 \mu\text{g C egg}^{-1}$ ) (**Fig. 5**). The mean ( $\pm$  SE) values of these parameters are  
331 provided in **Table IV**.



## 332 Discussion

333 Here we show that *Oithona similis* and *Calanus helgolandicus* exhibit contrasting responses to  
334 environmental variation at station L4, measured as differences in Egg Production Rate (EPR), adult  
335 female and egg carbon mass, and adult female and copepodite abundance. *O. similis* EPR appears to  
336 be more influenced by the physical environment, being significantly related to Sea Surface  
337 Temperature (SST) and Net Heat Flux (NHF), whereas physical and trophic parameters both seem  
338 to drive *C. helgolandicus* EPR, specifically Net Heat Flux (NHF), and diatom and heterotrophic  
339 dinoflagellate biomass. We also discovered a greater relative reduction in body mass with  
340 increasing SST over the season in *C. helgolandicus* compared to *O. similis*. Finally, we show that  
341 the timing of EPR and adult female and copepodite abundance maxima were decoupled in both  
342 species, a result that has implications for defining a single set of optimal conditions, or predictors,  
343 for maximum population fitness in either species.

## 344 Seasonality of egg production, egg size, and female size

345 Egg-brooding, ambush feeding predators typically have lower fecundity than broadcast spawning,  
346 active feeders (Sabatini and Kiørboe, 1994; Nielsen and Sabatini, 1996; Hirst and Kiørboe, 2002).  
347 Our study supports this, reporting low mean EPR in *Oithona similis* (1.73 eggs female<sup>-1</sup> d<sup>-1</sup>),  
348 compared to *Calanus helgolandicus* (15.11 eggs female<sup>-1</sup> d<sup>-1</sup>). Indeed, the data (**Table IV**) suggest  
349 that *C. helgolandicus* contribute more carbon, as a proportion of female body mass, into their eggs  
350 (Pond *et al.*, 1996). However, the proportional change of EPR over an annual cycle was broadly  
351 similar between the two species, with an approximate 8 to 10-fold range, and coefficients of  
352 variation of 73.6% and 89.7%, for *C. helgolandicus* and *O. similis*, respectively. The similarity in  
353 relative EPR variability between these species over the annual cycle contrasts with a series of  
354 papers suggesting that EPR of brooding species is more stable throughout the year, compared to that  
355 of broadcast spawners (Sabatini and Kiørboe, 1994; Nielsen and Sabatini, 1996). Although weak  
356 seasonality in *O. similis* EPR has previously been reported (Fransz and Gonzalez, 1995; Castellani

357 *et al.*, 2005a; 2007), these studies sampled over an incomplete annual cycle, hence the variation in  
358 the analysis could have had a seasonal bias. Seasonality in *O. similis* reproduction has indeed been  
359 reported in studies focused on a single site, in the Barents Sea (Dvoretsky and Dvoretsky, 2009a),  
360 the Arctic (Lischka and Hagen, 2005), and the North Sea (Drif *et al.*, 2010). However, we  
361 acknowledge that studies on a single species and site, as in our present study, do not provide  
362 sufficient evidence to reject the general rule that EPR in egg brooding copepods is more stable  
363 relative to broadcast spawning species (see Fig. 2. in Bunker and Hirst, 2004). Previous studies at  
364 L4 provide evidence of seasonality in *C. helgolandicus* EPR (Pond *et al.*, 1996; Irigoien *et al.*,  
365 2000a,b; Irigoien and Harris, 2003; Rey-Rassat *et al.*, 2004; Maud *et al.*, 2015).

366 For *Oithona similis*, neither egg carbon mass or diameter showed any clear seasonality at  
367 L4, which is similar to that reported for *O. similis* egg diameter in North Atlantic (Castellani *et al.*,  
368 2005a; 2007) and Greenland (Zamora-Terol *et al.*, 2013) populations. However, in the Barents Sea,  
369 *O. similis* egg diameter correlated positively with female prosome length (Dvoretsky and  
370 Dvoretsky, 2009a) and negatively with clutch size (Dvoretsky and Dvoretsky, 2009a,b).  
371 Conversely, *Calanus helgolandicus* egg carbon mass and female carbon mass followed similar  
372 trends, both reaching maximum values in spring (**Fig. 5**).

373 Our results show a stronger percent change in female carbon mass (Cf) per °C of seasonal  
374 warming in *Calanus helgolandicus* compared to *Oithona similis* (**Fig. 6**), with mean ( $\pm$  95% CI)  
375 values of -7.46 ( $\pm$  1.6)% and -2.33 ( $\pm$  0.5)% for *C. helgolandicus* and *O. similis*, respectively.  
376 Similarly, Horne *et al* (2016) report that on average calanoid copepods exhibit a 4-fold greater  
377 reduction in percent change in adult body mass per °C, with a mean ( $\pm$  95% CI) of -3.66 ( $\pm$  0.70)%,  
378 compared to cyclopoids with a mean of -0.91 ( $\pm$  0.59)%. This difference in temperature induced  
379 body size responses between calanoid and cyclopoid species has been attributed to contrasting  
380 feeding modes, as opposed to reproductive strategy (Horne *et al.*, 2016). With rates of food  
381 acquisition and resource use proposed to scale with body size differently between feeding strategies

382 (Horne *et al.*, 2016). Furthermore, feeding mode is associated with metabolic rate (Kiørboe and  
383 Hirst, 2014), which differs substantially between active feeders and passive feeders (Kiørboe,  
384 2011), and may also be a factor determining temperature-induced body size responses.

### 385 **Physical effects on egg production rate**

386 Despite the proportional change in EPR over the year being similar for both species, we propose  
387 that different factors influence the timing of EPR maxima in each species. In support of our first  
388 hypothesis, we found a stronger relationship between EPR and SST in *Oithona similis* compared to  
389 *Calanus helgolandicus*. The relationship between *O. similis* EPR and SST may in part be due to a  
390 temperature-dependent brooding period, whereby EPR is limited by the delay in production of new  
391 egg clutches until previous eggs hatch (Ward and Hirst, 2007). Since embryonic development rate  
392 increases with temperature, the time from the production of one clutch to the production of the next  
393 should decrease with increasing temperature (Nielsen *et al.*, 2002). This would result in the strong  
394 positive relationship between EPR and temperature that we observed, especially under food  
395 saturated conditions. Positive correlation between temperature and EPR has also been reported for  
396 *O. similis* populations in the Barents Sea (Dvoretsky and Dvoretsky, 2009a,b) and Greenland  
397 (Zamora-Terol *et al.*, 2014). In a synthesis of such rates, Ward and Hirst (2007) show the significant  
398 positive correlation between EPR and temperature in natural populations of *O. similis* (see their Fig.  
399 6).

400 In contrast, reproduction in broadcast spawning *Calanus helgolandicus* does not require a  
401 brooding period, as eggs are released directly into the sea. This could partially explain why SST is  
402 a poorer predictor of *C. helgolandicus* EPR, both in our study, and previous studies at L4 (Laabir *et*  
403 *al.*, 1998; Bautista *et al.*, 1994; Pond *et al.*, 1996; Irigoien *et al.*, 2000b; Bonnet *et al.*, 2005). NHF  
404 explained more of the variation in *C. helgolandicus* EPR, which peaked following the transition to  
405 positive NHF in spring (**Fig. 1**). This relationship between EPR and NHF becomes significant at ~  
406 50 W m<sup>-2</sup> (**Fig. 7**). At this time of year, SST is still relatively low, and the water column stratified.

407 The relationship between *C. helgolandicus* EPR and NHF could be due to the influence of NHF  
408 over the timing of the spring bloom (Smyth *et al.*, 2010; 2014), during which increased  
409 phytoplankton prey biomass could sustain maximum reproductive output. The same cannot be said  
410 for the relationship between *Oithona similis* EPR and NHF, considering this does not become  
411 significant until positive NHF into the water column has peaked at  $\sim 200 \text{ W m}^{-2}$  (**Fig. 3**). This peak  
412 is later in the year, and when water column stratification will be starting to breakdown. Water  
413 column stratification was found to be the only physical variable to correlate with *C. helgolandicus*  
414 population increase at L4 (Maud *et al.*, 2015). Eggs of broadcast spawning *Calanus* spp. die quickly  
415 upon contact with sediment (Uye, 2000). Therefore, water column stratification may also be  
416 important for retaining *C. helgolandicus* eggs in the upper mixed layer (Irigoien and Harris, 2003),  
417 although this could make the eggs more visible to predators (Eiane *et al.*, 2002). Furthermore, water  
418 column stratification may support *C. helgolandicus* prey detection and capture (Kiørboe and Saiz.,  
419 1995). The effect of turbulence on foraging efficiency in zooplankton has been well studied (Visser  
420 *et al.*, 2009), but further research into the effects of stratification on recruitment success in  
421 broadcast spawning copepods would be highly beneficial.

## 422 **Prey effects on egg production rate**

423 Our second hypothesis was that due to the contrast in feeding mode, *Oithona similis* EPR would  
424 have a stronger relationship with the biomass of motile prey, whereas *Calanus helgolandicus* EPR  
425 would have a stronger relationship with non-motile, diatom prey. Our data provide mixed support  
426 for this hypothesis. What we actually find is that *O. similis* EPR was not significantly related with  
427 any of the prey taxa considered. In contrast, *C. helgolandicus* EPR was significantly related with  
428 diatom biomass and also, to a lesser extent, heterotrophic dinoflagellates. Diatoms, ciliates, and  
429 heterotrophic dinoflagellates have previously been shown to sustain *C. helgolandicus* EPR at L4  
430 (Pond *et al.*, 1996; Irigoien *et al.*, 2000a,b; Fileman *et al.*, 2010). Thus, it is likely that this copepod  
431 species consumes both motile and non-motile prey throughout the year according to availability.

432 For example, *C. helgolandicus* have been shown to graze predominantly on diatoms during the  
433 spring bloom, but are more dependent on protozooplankton later in the year once diatom biomass  
434 decreases (Fileman *et al.*, 2007). As heterotrophic dinoflagellate biomass peaks in summer,  
435 following the spring diatom bloom (**Fig. 2**), *C. helgolandicus* may consume these dinoflagellates  
436 during times of the year when diatom biomass is low, as previously reported (Irigoien *et al.*,  
437 2000a,b; Fileman *et al.*, 2010). Although we found no statistically significant relationship between  
438 *C. helgolandicus* EPR and [Chl *a*], EPR for this species increases during the spring peak in [Chl *a*]  
439 (**Fig. 2**), as has been found previously at L4 (Bautista *et al.*, 1994; Pond *et al.*, 1996; Laabir *et al.*,  
440 1998; Bonnet *et al.*, 2005; Maud *et al.*, 2015). Overall, the longer *C. helgolandicus* time series  
441 suggested that food can be an important factor influencing fecundity, yet the shorter *O. similis* time  
442 series was unable to explain these dynamics.

443 Environmental seasonality can influence energy allocation in organisms, with the  
444 investment of energy under stressful conditions going towards survival, resulting in reduced  
445 fecundity (Kiørboe *et al.*, 2015). The fact that *Oithona similis* is reproductively active throughout  
446 the year is indicative of efficient energy uptake and assimilation. We retained [Chl *a*] in our model  
447 for *O. similis* EPR in order to maintain a trophic interaction term. In general, [Chl *a*] is a good  
448 proxy for phytoplankton biomass, and *O. similis* EPR did show a marginal relationship with [Chl *a*]  
449 (**Fig. 3**), a finding also reported in previous studies (Sabatini and Kiørboe, 1994; Castellani *et al.*,  
450 2007; Ward and Hirst, 2007; Drif *et al.*, 2010). *O. similis* fecundity has been shown to remain  
451 relatively high at low [Chl *a*] (Ward and Hirst, 2007), and weight-specific fecundity and growth in  
452 *Oithona* spp. is saturated at low [Chl *a*] (Hirst and Bunker, 2003), which could potentially explain  
453 the marginal significance observed here between *O. similis* EPR and [Chl *a*] at low chlorophyll  
454 concentrations (**Fig. 3, Table III**).

#### 455 **Decoupled seasonality in egg production and copepod abundance**

456 The annual timing of EPR and adult female and juvenile copepodite abundance maxima was  
457 decoupled in both species (**Fig. 4**). Decoupled EPR and abundance seasonality has previously been  
458 reported for *Calanus helgolandicus* at L4 (Pond *et al.*, 1996; Irigoien and Harris, 2003; Rey-Rassat  
459 *et al.*, 2004; Maud *et al.*, 2015), and for *Oithona similis* in the Arctic (Lischka and Hagen, 2005).  
460 Our observation of maximum *O. similis* female abundance in spring is consistent with a previous  
461 study of this species at L4 (Castellani *et al.*, 2016), and contradicts the notion that ambush feeders  
462 thrive during periods when motile prey predominates (Kenitz *et al.*, 2017). The decoupled  
463 seasonality of EPR and abundance could be explained by variation in mortality rates (Hirst and  
464 Kiørboe, 2002). Mortality rates of *C. helgolandicus* at L4 show strong seasonality, and are highest  
465 among early developmental stages (Hirst *et al.*, 2007). Consequently, EPR is a poor predictor of  
466 abundance in later developmental stages. Mismatch between seasonality in egg production and egg  
467 viability can lead to eggs being produced in sub-optimal conditions for peak egg fitness (Varpe *et al.*,  
468 2007), with negative consequences on recruitment success. The fact that optimum conditions for  
469 reproduction and adult female and copepodite abundance maxima occur at different times of year,  
470 under different temperature and food conditions, has implications for niche modelling approaches  
471 which only use species abundance as a function of environmental parameters, to represent an  
472 ecological niche (Helaouët *et al.*, 2013).

473 Rate of maturation from eggs to adults should determine the time period between maximum  
474 reproductive output and increased adult abundance, assuming high recruitment success of the  
475 population. *Calanus helgolandicus* may take longer to develop than *Oithona similis*, as  
476 development time from egg to adult at 15°C was estimated at 24 - 40 days in *C. helgolandicus*  
477 (Bonnet *et al.*, 2009), and ~ 20 days in *O. similis* (Sabatini and Kiørboe, 1994). The fact that adult  
478 female abundance did not increase until long after the period of maximum EPR, despite their  
479 relatively short development times, confirms that there are indeed other factors, such as mortality  
480 and advection (Irigoien and Harris, 2003; Hirst *et al.*, 2007), influencing copepod abundance.  
481 Ohman and Hirche (2001) present evidence for density-dependent mortality in an oceanic

482 population of *Calanus finmarchicus*, whereby egg mortality rates were a function of adult female  
483 and copepodite abundance. Likewise, density-dependence in egg mortality rates, with higher  
484 mortality rates observed at higher adult densities, have been reported for the *C. helgolandicus*  
485 population at station L4 (Hirst *et al.*, 2007). Thus predation, by cannibalism or from other species,  
486 combined with egg hatching success (Maud *et al.*, 2015), may also contribute to decoupled  
487 seasonality in egg production and copepod abundance.

#### 488 **Statistical analysis and development of predictive models**

489 One limitation of our study was the shorter period over which we have data for *Oithona similis*, and  
490 the restrictions this imposed on including an autoregressive noise process as part of the Generalised  
491 Additive Mixed Model (GAMM). The benefit of having the longer *Calanus helgolandicus* record  
492 was that it represents the L4 physical and trophic interactions with EPR over a longer time scale.  
493 Whilst the *O. similis* record is short, this species has been exposed to the same physical  
494 environment as for *C. helgolandicus*, and so we can discuss both taxa in the longer term context.  
495 Further work can be pursued using these dynamic relationships to help establish a predictive model  
496 for *O. similis*.

## 497    **Conclusion**

498    Contrasting traits of feeding mode, reproductive strategy, and body size, between *Oithona similis*  
499    and *Calanus helgolandicus*, appear to induce different responses in both reproduction and  
500    abundance to environmental variation at L4. The fact that optimum conditions for reproduction and  
501    abundance of these copepod species occurred at different times of year, under differing temperature  
502    and food conditions, is relevant to niche modelling approaches. Our results therefore demonstrate  
503    that optimum population performance cannot be defined by a single set of environmental  
504    conditions. Overall, understanding how contrasting functional traits translate into seasonality of  
505    reproduction, abundance, and body size can enhance our ability to predict how species might  
506    perform under different climatic scenarios.



## 507    **Acknowledgements**

508    L. E. Cornwell was funded by the NERC GW4+ Doctoral Training Partnership. We would like to  
509    acknowledge the NERC National Capability in supporting the Western Channel Observatory L4  
510    time series. Further funding came from the Natural Environment Research Council and Department  
511    for Environment, Food and Rural Affairs [grant number NE/L003279/1, Marine Ecosystems  
512    Research Programme]. Non-linear system identification components of this work were supported by  
513    J. T. Bruun in a personal scientific capacity. We thank D. V. P. Conway for his guidance on  
514    copepod identification, G. Simpson for his advice with statistical analysis, J. R. Fishwick for  
515    providing the CTD data, R. L. Airs and D. G. Cummings for providing the Chlorophyll *a* data, and  
516    the crew of the RV *Plymouth Quest*. We also thank the British Atmospheric Data Centre for  
517    providing the ECMWF operational and ERA-40 datasets. Finally, we would like to thank the  
518    reviewers for providing such detailed and constructive advice, greatly improving the paper.

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## Figure Legends

**Fig. 1:** Mean ( $\pm$  SE) for (a) *Oithona similis* Egg Production Rate (EPR) and mass-specific EPR (SEPR) (2011 – 2016) (b) *O. similis* EPR and Sea Surface Temperature (SST) (2003; 2011 – 2016) (c) *O. similis* EPR and Net Heat Flux (NHF) (2003; 2011 – 2016) (d) *Calanus helgolandicus* EPR and SEPR (1994), carbon mass values from Pond *et al* (1996) (e) *C. helgolandicus* EPR and SST (1992 – 2016) (f) *C. helgolandicus* EPR and NHF (1992 – 2016).

**Fig. 2:** Mean ( $\pm$  SE) for (a) Phytoplankton biomass seasonality over the period of the *Oithona similis* dataset (2003; 2011 – 2014) (b) Zooplankton biomass seasonality over the period of the *O. similis* dataset (2003; 2011 – 2014) (c) *O. similis* EPR and Chlorophyll *a* concentration [Chl *a*] (2003; 2011 – 2016) (d) Phytoplankton biomass seasonality over the period of the *Calanus helgolandicus* dataset (1992 – 2014) (e) Zooplankton biomass seasonality over the period of the *C. helgolandicus* dataset (1992 – 2014) (f) *C. helgolandicus* EPR and [Chl *a*] (1992 – 2016). Aut.dino = Autotrophic dinoflagellate, Pflag = Phytoflagellate, Het.dino = Heterotrophic dinoflagellate, Zflag = Zooflagellate. Coccolithophores were excluded from this figure due to their low biomass at L4.

**Fig. 3:** Plots showing the non-parametric contributions for each environmental factor included in the Generalised Additive Mixed Model (GAMM) on Egg Production Rate (EPR) for the *Oithona similis* dataset (2011 - 2016). (a) Sea Surface Temperature (SST, °C) (b) Net Heat Flux (NHF, W m<sup>-2</sup>) (c) Chlorophyll *a* concentration ([Chl *a*], µg L<sup>-1</sup>). Horizontal line at  $y = 0$  marks where there is no 'non-linear effect' of the 'x' variable on EPR. Both solid and dashed lines above the  $y = 0$  line indicates a significant positive relationship. Dashed lines represent uncertainty interval.

**Fig. 4:** Mean ( $\pm$  SE) for (a) *Oithona similis* female abundance (Female Ab) and Egg Production Rate (EPR) (2011 – 2016) (b) *O. similis* copepodite abundance (Copepodite Ab) and egg sac abundance (Egg sac Ab) (2011 – 2016) (c) *Calanus helgolandicus* female abundance (Female Ab)

736 and EPR (1992 – 2016) (d) *C. helgolandicus* copepodite abundance (Copepodite Ab) (1992 –  
737 2016).

738 **Fig. 5:** Mean ( $\pm$  SE) for (a) *Oithona similis* female carbon mass (Cf) and Sea Surface Temperature  
739 (SST) (2011 – 2016) (b) *O. similis* Cf and egg carbon mass (Ce) (2011 – 2016) (c) *Calanus*  
740 *helgolandicus* Cf and SST (March – September 1994) (d) *C. helgolandicus* Cf and Ce (March –  
741 September 1994). Carbon mass data for *C. helgolandicus* was derived from Pond *et al* (1996).

742 **Fig. 6:** Female body carbon (Cf) of *Oithona similis* and *Calanus helgolandicus* against Sea Surface  
743 Temperature (SST). Note the y-axes are both Log<sub>10</sub> scales. Carbon mass data for *C. helgolandicus*  
744 from Pond *et al* (1996), measured over March – September, 1994. *O. similis* carbon mass data from  
745 the present study over 2011 – 2016. The regressions of body size are described by the equations:  
746 Log<sub>e</sub> *O. similis* Cf = - 0.0236 SST - 0.7197 ( $R^2_{adj}$  = 0.35,  $P$  < 0.0001,  $n$  = 132), and Log<sub>e</sub> *C.*  
747 *helgolandicus* Cf = - 0.0775 SST + 4.8021 ( $R^2_{adj}$  = 0.76,  $P$  < 0.0001,  $n$  = 28).

748 **Fig. 7:** Plots showing the non-parametric contributions for each environmental factor included in  
749 the Generalised Additive Mixed Model (GAMM) on the Egg Production Rate (EPR) for the  
750 *Calanus helgolandicus* dataset (1992 - 2016). (a) Net Heat Flux (NHF, W m<sup>-2</sup>) (b) Diatom biomass  
751 (mg C m<sup>-3</sup>) (c) Heterotrophic dinoflagellate biomass (Hetdino, mg C m<sup>-3</sup>). Horizontal line at  $y = 0$   
752 marks where there is no 'non-linear effect' of the 'x' variable on EPR. Both solid and dashed lines  
753 above the  $y = 0$  line indicates a significant positive relationship. Dashed lines represent uncertainty  
754 interval.

## 755 Tables

756

757 **Table I:** Western Channel Observatory (WCO) time series data 1992 – 2016; length of datasets available and  
758 analysed for each parameter, and the sampling method used to obtain the data.

759

Parameter	Years analysed	Sampling method
<i>Oithona similis</i> abundance	Nov 2011 – Dec 2016. Excluding Mar 2014 - Jun 2015	2011 – 2014: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 4% buffered formalin. 2015 – 2016: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 2% acid Lugol's solution.
<i>Oithona similis</i> egg production	2003; Nov 2011 – Dec 2016. Excluding Mar 2014 - Jun 2015	2003: ring net (50 µm mesh, 50 cm diameter), 0 – 50 m, fixed in 4% buffered formalin. 2011 – 2014: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 4% buffered formalin. 2015 – 2016: ring net (63 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 2% acid Lugol's solution.
<i>Calanus helgolandicus</i> abundance	Feb 1992 – Dec 2016. Excluding Sept – Dec 2005	WP2 net (200 µm mesh, 57 cm diameter), 0 – 50 m, fixed in 4% buffered formalin.
<i>Calanus helgolandicus</i> egg production	Feb 1992 – Dec 2016. Excluding Aug 2006 – Sept 2007	1992 – 2016: live samples, ring net (710 µm, 45 cm diameter ), oblique tow 0 - 10 m.
Sea Surface Temperature	Feb 1992 – Dec 2016	1992: Mercury in glass thermometer. 1993 – 2002: CTD sensors. 2002 – 2016: SeaBird SBE 19+ CTD.
Net Heat Flux	Feb 1992 – Dec 2016	Meteorological parameters obtained from the European Centre for Medium Range Weather Forecasting (ECMWF) operational and ERA-40 datasets, provided by the British Atmospheric Data Centre.
Surface Chlorophyll <i>a</i> Concentration	Feb 1992 – Dec 2016	100 mL surface seawater filtered through 25 mm GF/F filters in triplicate, extracted in 90% acetone at 4 °C. Analysed by Turner fluorometry following Welschmeyer (1994) protocol.
Phytoplankton and protozooplankton biomass	Oct 1992 – Dec 2014. Excluding Oct 1994 – May 1995	10 L Niskin bottle, 10 m, 200 mL sub-sample fixed in 2% acid Lugol's solution.

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761

762 **Table II:** *Oithona similis* egg production and carbon mass equations. E = Egg abundance (ind m<sup>-3</sup>), F =  
763 Female abundance (ind m<sup>-3</sup>), HT = Time from laying to hatching (days), T = Temperature (°C), PL =  
764 Prosome Length (µm), ED = Egg Diameter (µm). The ‘slope’ in the equation of Forster *et al* (2012) is that  
765 from the relationship between Log<sub>e</sub> mass and temperature (°C).

766

Parameter	Equation	Reference
Egg Production Rate (EPR, eggs female <sup>-1</sup> d <sup>-1</sup> )	$EPR = E / (F * HT)$	Edmondson <i>et al</i> (1962); Checkley (1980)
Hatch Time (HT, d <sup>-1</sup> )	$HT = 1504.5 (T + 7.6998)^{-2.05}$	Bělehrádek equation using parameters described for <i>O.</i> <i>similis</i> by Nielsen <i>et al</i> (2002).
Hatching Rate (HR, d <sup>-1</sup> )	$HR = 1 / [1504.5 (T + 7.6998)^{-2.05}]$	Bělehrádek equation using parameters described for <i>O.</i> <i>similis</i> by Nielsen <i>et al</i> (2002).
Female carbon mass (Cf, µg C female <sup>-1</sup> )	$Cf = 10^{(1.45 * (\text{Log PL}) - 4.25)}$	Uye (1982)
Egg carbon mass (Ce, µg C egg <sup>-1</sup> )	$Ce = 5.32 \times 10^{-8} * ED^{3.04}$	Uye and Sano (1995)
Mass-specific Egg Production Rate (SEPR, egg-C female-C <sup>-1</sup> d <sup>-1</sup> )	$SEPR = (E/F) HR (Ce/Cf)$	Sabatini and Kiørboe (1994)
Percent change in female carbon mass per °C (% °C <sup>-1</sup> )	$(e^{(\text{slope})} - 1) * 100$	Forster <i>et al</i> (2012)

767

768 **Table III:** Generalised Additive Mixed Model (GAMM) outputs for *Oithona similis* Egg Production Rate  
769 (EPR). SST = Sea Surface Temperature (°C), NHF = Net Heat Flux (W m<sup>-2</sup>), Chl *a* = Chlorophyll *a* (µg L<sup>-1</sup>).  
770 Each covariate is represented as a smooth function, s(x). EDF = Estimated Degrees of Freedom, Ref.df =  
771 Residual Degrees of Freedom. n = sample size.

772

773

Covariate	EDF	Ref.df	<i>F</i>	<i>P</i>	n
s(SST)	1.958	1.958	2.871	0.0438	217
s(NHF)	2.016	2.016	2.921	0.0622	217
s(Chl <i>a</i> )	1.485	1.485	1.421	0.1619	217

**Table IV:** Mean ( $\pm$  SE) and sample size (n) for: *Oithona similis* and *Calanus helgolandicus* Egg Production Rate (EPR), egg and female size, and mass specific EPR (SEPR). Years analysed: *O. similis* EPR (2003; 2011 – 2016), egg and female size, and SEPR (2011 – 2016); *C. helgolandicus* EPR (1992 – 2016), egg and female size, and SEPR (1994). *C. helgolandicus* carbon mass data obtained from Pond *et al* (1996). Spring = March – May, Summer = June – August, Autumn = September – October, Winter = December – February, PL = Prosome Length, Cf = female carbon mass, Ce = egg carbon mass, ES = number of eggs per sac.

Species	Season	Female PL ( $\mu\text{m}$ )	Cf ( $\mu\text{g C female}^{-1}$ )	Egg diameter ( $\mu\text{m}$ )	Ce ( $\mu\text{g C egg}^{-1}$ )	ES (eggs sac $^{-1}$ )	EPR (eggs female $^{-1}$ d $^{-1}$ )	SEPR (egg-C female-C $^{-1}$ d $^{-1}$ )
<i>Oithona similis</i>	Spring	456 $\pm$ 3.29 (30)	0.40 $\pm$ 0.004 (30)	61 $\pm$ 0.84 (30)	0.015 $\pm$ 0.001 (30)	9.77 $\pm$ 0.33 (30)	1.66 $\pm$ 0.18 (33)	0.057 $\pm$ 0.008 (30)
	Summer	425 $\pm$ 3.17 (37)	0.36 $\pm$ 0.004 (37)	59 $\pm$ 0.71 (32)	0.013 $\pm$ 0.001 (32)	9.28 $\pm$ 0.21 (32)	2.67 $\pm$ 0.37 (42)	0.113 $\pm$ 0.018 (31)
	Autumn	403 $\pm$ 3.32 (37)	0.34 $\pm$ 0.004 (37)	60 $\pm$ 0.63 (36)	0.014 $\pm$ 0.0004 (36)	6.93 $\pm$ 0.25 (37)	1.56 $\pm$ 0.28 (39)	0.061 $\pm$ 0.011 (35)
	Winter	420 $\pm$ 4.33 (28)	0.36 $\pm$ 0.005 (28)	59 $\pm$ 0.92 (27)	0.013 $\pm$ 0.001 (27)	6.68 $\pm$ 0.36 (27)	0.78 $\pm$ 0.17 (32)	0.032 $\pm$ 0.007 (27)
<i>Calanus helgolandicus</i>	Spring		59.57 $\pm$ 2.54 (10)		0.468 $\pm$ 0.04 (10)		21.38 $\pm$ 0.71 (244)	0.167 $\pm$ 0.02 (10)
	Summer		36.92 $\pm$ 1.29 (14)		0.311 $\pm$ 0.01 (13)		21.08 $\pm$ 0.64 (256)	0.189 $\pm$ 0.02 (13)
	Autumn						9.74 $\pm$ 0.45 (230)	
	Winter						5.77 $\pm$ 0.44 (200)	



779 **Table V:** Generalised Additive Mixed Model (GAMM) outputs for *Calanus helgolandicus* Egg Production  
780 Rate (EPR). NHF = Net Heat Flux ( $\text{W m}^{-2}$ ), Diatom = Diatom Biomass ( $\text{mg C m}^{-3}$ ), Hetdino = Heterotrophic  
781 Dinoflagellate Biomass ( $\text{mg C m}^{-3}$ ). Each covariate is represented as a smooth function  $s(x)$ . EDF =  
782 Estimated Degrees of Freedom, Ref.df = Residual Degrees of Freedom. n = sample size.

Covariate	EDF	Ref.df	$F$	$P$	n
s(NHF)	2.522	2.522	9.985	< 0.0001	1081
s(Diatom)	3.644	3.644	4.454	0.00304	1081
s(Hetdino)	2.613	2.613	3.288	0.05366	1081

783